

Species-specific responses of planktivorous fish to the introduction of a new piscivore: implications for prey fitness

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SUMMARY

1. Antipredator behaviour by the facultative planktivorous fish species roach (*Rutilus rutilus*), perch (*Perca fluviatilis*) and rudd (*Scardinius erythrophthalmus*) was studied in a multi-year whole-lake experiment to evaluate species-specific behavioural and numerical responses to the stocking of pikeperch (*Sander lucioperca*), a predator with different foraging behaviour than the resident predators large perch (*P. fluviatilis*) and pike (*Esox lucius*).
2. Behavioural responses to pikeperch varied greatly during the night, ranging from reduced activity (roach and small perch) and a shift in habitat (roach), to no change in the habitat use and activity of rudd. The differing responses of the different planktivorous prey species highlight the potential variation in behavioural response to predation risk from species of similar vulnerability.
3. These differences had profound effects on fitness; the density of species that exhibited an antipredator response declined only slightly (roach) or even increased (small perch), whereas the density of the species that did not exhibit an antipredator response (rudd) decreased dramatically (by more than 80%).
4. The maladaptive behaviour of rudd can be explained by a 'behavioural syndrome', i.e. the interdependence of behaviours expressed in different contexts (feeding activity, antipredator) across different situations (different densities of predators).
5. Our study extends previous studies, that have typically been limited to more controlled situations, by illustrating the variability in intensity of phenotypic responses to predators, and the consequences for population density, in a large whole-lake setting.

Keywords: fixed behaviour, habitat preference, multiple predator, multiple prey, phenotypic plasticity

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Introduction

Species can respond to predation risk by modifying their phenotype (e.g. behavioural and morphological adaptations, reviewed in Lima & Dill, 1990; Tollrian & Harvell, 1999). This flexibility has clear benefits for

fitness in habitats in which predation risk is spatially and temporally variable (Stearns, 1989; Houston, McNamara & Hutchinson, 1993; Werner & Anholt, 1993). A variety of behavioural modifications may reduce predation risk, including a decline in activity and changes in habitat preference (Ives & Dobson, 1987; Lima, 1998). Understanding such relationships is important, because changes in prey behaviour can substantially influence community dynamics and biogeochemical processes (Werner & Peacor, 2003; Schmitz, Krivan & Ovadia, 2004; Stief & Hölker, 2006).

Recent studies have shown that different prey demonstrate different behavioural responses to new predators. This could result from phylogenetic inertia, naïvety to introduced predators or behavioural syndromes (Sih, Kats & Maurer, 2000; Caudill & Peckarsky, 2003; Sih, Bell & Johnson, 2004). In addition, we are beginning to understand how prey respond to multiple predators. Multiple predator species feeding on a common prey can lead to higher or lower predation than would be expected simply by combining their individual effects (Relyea, 2003).

Most of the behavioural studies have been conducted in short-term laboratory, mesocosm or enclosure experiments (Lima, 1998), and therefore, studies conducted at spatiotemporal scales closer to nature are needed to extend the findings obtained at smaller scales (Carpenter, 1996; Persson *et al.*, 1996; Biro, Post & Parkinson, 2003). We do not know, for example, if a prey that is already subject to several predators in a large and complex field setting will respond at all to the introduction of an additional predator. It is possible that, in the field, prey exhibit more generalized responses because they cannot differentiate cues from the various predators and other environmental factors.

Here, we examined the response of three prey of similar vulnerability to a predator introduced experimentally into a lake with two other resident predators. Isolated small lakes are particularly appropriate for whole-system ecological experiments, because predator density can be manipulated and the behavioural responses of the prey can be monitored (Carpenter & Kitchell, 1993). Furthermore, the experiments can be conducted at natural temporal and spatial scales so that realistic data can be collected, even if experimental replicates or otherwise identical lakes serving as control are lacking (Carpenter, 1990).

Shallow lakes consist mainly of two habitats with differing resource densities and predation risks (Scheffer, 1998). The littoral zone offers refuge from predation, because of structural diversity, and provides benthic food resources. The pelagic habitat is more risky, but can also be more profitable for planktivorous fish, if the zooplankton densities are higher than in the littoral zone (Hölker *et al.*, 2002).

As is typical for many lakes of the European Central Plains (Mehner *et al.*, 2005), the planktivores in our study consist of roach (*Rutilus rutilus* L.), small perch (*Perca fluviatilis* L.) and rudd (*Scardinius erythrophthalmus* L.). Roach feed mainly on zooplankton but also ingest macrozoobenthos, macrophytes and algae (Lammens & Hoogenboezem, 1991). Perch are also known to feed on zooplankton when young, but undergo an ontogenetic niche shift towards a diet of benthic organisms and even fish when older (Persson, 1986). Finally, rudd normally ingest large amounts of macrophytes and filamentous algae in addition to zooplankton (Lammens & Hoogenboezem, 1991). With respect to predation, the vulnerability of roach, small perch and rudd (6–16 cm) can be considered similar because of their similar morphology (streamlined shape) and ecology (facultative planktivores) which may determine the optimal set of corresponding behavioural antipredator responses.

We compared two periods in the whole-lake experiment to assess the species-specific behavioural response to predation risk. In the first period, the piscivorous guild consisted only of pike (*Esox lucius* L.) and large (>20 cm) perch, a predator combination typical for small mesotrophic lakes (Mehner *et al.*, 2005). Both indigenous predators are mainly day active. Pike is a solitary sit and wait predator in the littoral zone, whereas large perch hunt in groups in the pelagic zone (Craig, 1987, 1996). In lakes with this piscivorous guild, several prey fish species undertake diel horizontal migrations between the relatively safe littoral habitats during daytime towards the more risky, but also more profitable, pelagic habitats at night (Haertel, Baade & Eckmann, 2002; Reeb, 2002; Gliwicz, Slon & Szynek, 2006). Prior to the second period, pikeperch (*Sander lucioperca* L.) were stocked into the lake. This species is most active at dawn and dusk and at night, when they forage in the pelagic zone (Craig, 1987). Thus, pikeperch stocking mainly increased the predation risk in the pelagic zone during the night. If prey fish responded

adaptively, stocking of pikeperch should induce a change in their migration and activity, with these behavioural modifications expected to be strongest during the night because day active predators were already present (cf. Hölker *et al.*, 2002; Hölker & Mehner, 2005).

Here, we asked (i) whether the introduction of pikeperch would induce a shift in the night time distribution of roach, small perch and rudd towards an increased use of the littoral zone compared with the pelagic zone; (ii) whether the activity of the three planktivorous species would change in response to the overall increased predation risk and (iii) whether both behavioural traits (i.e. activity and habitat preference) would vary between species. We predicted that the strength of any behavioural response would be negatively correlated with the reduction in density because of predation.

Methods

Study site

Lake Großer Vätersee is a mesotrophic lake in the Baltic lake region of northeast Germany (53°00'N; 13°33'E, 60 m.a.s.l.; area, 12 ha; max. depth, 11.5 m; mean depth, 5.2 m; volume, 633 000 m³). Details of its hydrography, trophic characteristics, species composition and cover of submerged macrophytes, and a preliminary characterization of the pelagic food web structure are provided in Kasprzak *et al.* (2000). Details of densities and habitat use of top predators are provided in Haertel *et al.* (2002) and Schulze *et al.* (2006a). In the period 1997/98, before the introduction of pikeperch (referred hereafter to as the 'pikeperch absent period', PAP), roach and perch were the dominant fish species in terms of numbers and biomass (Haertel *et al.*, 2002). Pike and large perch (>20 cm total length, TL) were the top predators in this period (Haertel *et al.*, 2002). The total biomass of piscivorous fish in this PAP was 226 and 223 kg in 1997 and 1998, respectively (Schulze *et al.*, 2006a). The median TL (minimum–maximum) of pike was 36.0 (5.0–101.0) cm in the PAP, and 32.0 (12.5–92.0) cm in 2001/02 (referred hereafter to as the 'pikeperch present period', PPP), whereas the median length of piscivorous perch was 27.5 (20.5–39.5) cm and 28.0 (20.5–7.0) cm in the PAP and the PPP, respectively. In spring 2001, 782 (184 kg) age-2 pikeperch were

released. A further 301 (101 kg) pikeperch were introduced in spring 2002. The median length of pikeperch released was 34.0 (28.0–49.0) cm in 2001 and 38.5 (29.5–55.0) cm in 2002. As a result of the pikeperch stocking, lake-wide piscivorous fish biomass rose to 320 kg (31% pikeperch) in 2001 and to 366 kg (22% pikeperch) in 2002 (Schulze *et al.*, 2006a). Pike biomass was relatively constant between 1997 and 2001 (134–156 kg), but increased significantly in 2002 (236 kg) because of a higher recruitment from larvae into the juvenile size classes (Schulze *et al.*, 2006a). The biomass of large perch never exceeded 96 kg and dropped below 50 kg in 2002 (Schulze *et al.*, 2006a). According to the owner of Lake Großer Vätersee, pikeperch had not occurred in the lake over the previous 100 years, and thus the prey were naïve to this predator.

According to gill net catches and electrofishing, pike predominantly inhabited the littoral zone in both periods (Haertel *et al.*, 2002; Schulze *et al.*, 2006a). During the daytime large perch almost exclusively used the pelagic zone in the PAP (Haertel *et al.*, 2002), but were found in both the pelagic (50%) and the littoral zones (50%) in the PPP. This behavioural change was probably a response to competition from pikeperch (Schulze *et al.*, 2006a). No large perch were caught by gill nets during the night in either period, indicating that large perch are generally not very active by night and had a lower catchability. About 70% of pikeperch were caught in the pelagic zone and 30% in the littoral zone by both day and night (Schulze *et al.*, 2006a).

In Lake Großer Vätersee, both perch and roach (6–16 cm) included a large amount zooplankton in the diet (Hölker *et al.*, 2002; Haertel *et al.*, 2002). Both species also consumed other invertebrates, but this category was usually not a prominent component of the diet in Lake Großer Vätersee. The littoral zone was not a very profitable foraging habitat, as macrozoobenthos and zooplankton generally reached only very low densities there overall (Hölker *et al.*, 2002), compared with the situation in more eutrophic systems (e.g. Hölker & Breckling, 2002; Okun & Mehner, 2005).

Pelagic and littoral resources

Because behavioural responses to changes in predation risk can be confounded by changes in resource density (Reebs, 2002), we measured the abundances of

pelagic and littoral food resources. Using a cone-shaped plankton net (length 1.2 m, opening diameter 0.027 m², mesh size 90 µm), triplicate vertical hauls from 0 to 10 m in the pelagic zone were taken every 2 weeks in both the PAP and the PPP. Because there is an anoxic zone below 7–9 m depth in the lake from late April to late October, zooplankton density refers to the epilimnetic volume from 0 to 7–9 m only. Littoral zooplankton was collected monthly at a water depth of 0.5 m in 1998, 2001 and 2002 with a Schindler trap at four sampling sites evenly distributed along the shoreline. Littoral macrozoobenthos was sampled at 0.5 and 3 m along three transects with an Ekman-Birge grab (15 × 15 cm). Sampling was conducted in May, August and October 1998, and monthly from May to October in 2001 and 2002. For all prey groups, annual averages were calculated from individual samplings over time.

Fish abundance and distribution

Individuals experience highly variable size-specific selection regimes in their vulnerability as prey during ontogeny (Ebenman, 1992). Thus, we focused only on specimens in the size range 6–16 cm, for which we predicted the strongest response in behaviour and density. Young-of-year fishes (<6 cm) are reported to have genetically fixed behavioural patterns (Post & McQueen, 1988; Byström *et al.*, 2003) and individuals >16 cm experience a reduced predation risk in Lake Großer Vätersee (Haertel *et al.*, 2002; Schulze *et al.*, 2006b; see also Dörner & Wagner, 2003; Dörner *et al.*, 2007).

Habitat use of the littoral (≤3 m water depth) and the pelagic zones by roach, small perch and rudd was investigated. Both habitats were sampled simultaneously by day and night. Sampling took place monthly from May to September 1997 and from May to October in 1998, 2001 and 2002 (*cf.* Haertel *et al.*, 2002). All fishing was carried out by gill nets of 8–15 mm mesh size (knot to knot; total of eight nets; overall length 105 m; 45 m littoral zone, 60 m pelagic zone). In the littoral zone, the nets were set at the bottom perpendicular to the shoreline. In the pelagic zone floating nets of 6-m depth were used, covering almost the entire epilimnion (the lake is thermally stratified from late April to late October, with an anoxic zone of up to 7-m water depth; Kasprzak *et al.*, 2000). The nets were set for 2 h during day (10:00–

12:00 hours) and during the night. Night-time sampling started immediately after sunset, and varied between 19:00–21:00 hours and 23:00–01:00 hours in the course of the year.

The fish were immediately stored on ice after capture, and their TL and wet mass (wm, 0.1 g) recorded. Catch per unit effort (CPUE) for each species was calculated as the number of fish per 100 m² net panel and 2 h exposure time. Proportionate habitat use by all prey species was calculated from CPUE values obtained simultaneously in the littoral and pelagic, separately for day and night periods. From these values, an annual average use of the littoral zone (% of total CPUE) was calculated. In order to avoid a bias because of some samples with extremely low numbers, we excluded from this calculation all samples where only one–three specimens per species were caught in total (12/178). Using a higher cut-off value did not change the qualitative nature of the results.

The abundances of roach, small perch and rudd were estimated by multiple mark-recapture experiments in 1998 and 2002. Fish were caught by electrofishing (Bretschneider Special Electronics, Chemnitz, Germany, EFG/400: 4 kW, 200–610 V, DC), anaesthetized (MS 222) and measured (TL, to the nearest 1 mm). All fish larger than 6 cm were tagged with coded wire tags (Northwest Marine Technology (NMT), Salisbury, MD, U.S.A.), which were injected into the dorsal musculature in 1998 (Haertel *et al.*, 2002) or into the head (snout tissue or cheek muscle) in 2002. In each electrofishing operation, all fish were checked for tags with a portable sampling detector (NMT), unmarked fish were tagged and all fish were released (*cf.* Dörner *et al.*, 2006). Population size was calculated according to model M_t (White *et al.*, 1982; Pollock *et al.*, 1990). Model M_t is a maximum likelihood estimator for multiple batch mark-recapture data that allows capture probability to vary by time (e.g. capture occasion). Biomass was derived from length–weight relationships obtained from Lake Großer Vätersee fish samples. In preliminary experiments we showed that the mortality of small fish after capture, anaesthesia and marking with coded wire tags at different water temperatures is low and independent of water temperature (Dörner *et al.*, 2006). To be on the safe side, these estimates were restricted to early spring (Haertel *et al.*, 2002). Moreover, a short time frame better approximates to the

assumption of a closed population in mark-recapture models.

Using CPUE values to compare fish activity between the PAP and the PPP may be misleading, as they reflect the absolute numbers of active fish and do not take into account potential changes in population size. Accordingly, we derived an activity coefficient that reflected the proportion of active fish in comparison to the population size. CPUE and population size (n) are related by:

$$\text{CPUE} = qn$$

where q is the catchability coefficient, i.e. the proportion of the total population caught by one unit of fishing effort (King, 1995). The catchability coefficient depends on both biological (fish activity and behaviour) and technological (gear type, design, size, colour and material, gear position, duration and handling) features. As we kept the technological component of q constant during experimental fishing, the catchability of the gill nets was directly proportional to the activity index A_i of the fish:

$$q \sim A_i$$

Further, n was calculated from the mark-recapture data, such that A_i could be calculated from the CPUE data (including samplings with <4 specimens per species) and directly be compared between the PAP and PPP.

The species composition of the 6–16 cm size class consumed by piscivores from May to October was recalculated from the data of Haertel *et al.* (2002) and Schulze *et al.* (2006a). Both authors calculated mean daily rations of piscivores with a computerized bioenergetics model (Fish Bioenergetics 3.0; Hanson *et al.*, 1997) where they used mean yearly mass increment per age or length class as somatic growth model input. The mean consumption estimates were expanded to population estimates by considering the relative abundances of the several age groups or length classes per species of piscivore.

Statistical analyses

Statistical significance was tested at the $P < 0.05$ level. The Kolmogorov–Smirnov test was applied to check, if data sets were normally distributed. Differences in the average abundance of planktivorous prey fish between the two periods were analysed by Student's

t -test. Differences in zooplankton and macrozoobenthos abundance between years were analysed by a Kruskal–Wallis test. Where significant differences were found, pairwise comparisons were performed using the Nemenyi test, a nonparametric multiple comparison method. The proportions of planktivorous prey fish observed in different habitats and their activity indices were analysed by Mann–Whitney U -tests.

Results

In both periods, mean zooplankton abundance (May–October) was generally higher in the pelagic than in the littoral zone (Table 1). *Daphnia* sp. was abundant in the pelagic zone in 2001, whereas the abundance of other, much smaller cladocerans decreased slightly in the pelagic zone in the PPP (Table 1). The abundance of insect larvae was significantly higher in 2002 and that of molluscs was significantly higher in both years of the PPP (Table 1). In contrast, the abundance of *Daphnia* sp. and other cladocerans was significantly lower in both years of the PPP (Table 1).

Population size of roach was 39% smaller in the PPP than in the PAP (Table 2). In contrast, the number of small perch was 36% higher in the PPP. The number of rudd decreased significantly by more than 80%. The daytime activity of roach and small perch did not differ between the PAP and the PPP, whereas nocturnal activity was significantly lower in the PPP (Table 3). No differences in the diel activity of rudd were observed between the PAP and the PPP (Table 3).

In the PAP, roach used only the littoral zone during the day but mainly the pelagic zone at night (Fig. 1). This was different at night in the PPP, when roach primarily used the littoral zone (Fig. 1; Table 4). In both the PPP and the PAP, small perch were exclusively found in the littoral zone during the day (Fig. 1; Table 4). In the PAP, they also used the littoral zone at night. Since only two small perch were caught at night in total in the entire PPP, the nocturnal habitat use of small perch could not be determined from the gill net catches. However, as population density increased slightly, and CPUEs of gill nets reflect only the active fish, this indicates an extreme reduction in activity of small perch at night. This was also corroborated by the results of nightly electrofishing, where high numbers of motionless small perch were observed in

Taxa/group	Year	LIT	n	Ne	P-value	PEL	n	Ne	P-value
<i>Daphnia</i> sp.	1997				0.032	9.7 (5.5–29.7)	12		0.193
	1998	1.5 (1.1–3.0)	6	a		27.1 (11.0–34.9)	13		
	2001	0.2 (0.1–0.7)	7	b		31.0 (10.1–39.6)	13		
	2002	0.2 (0.0–0.2)	6	b		17.2 (8.2–20.9)	13		
Other cladocerans	1997				0.049	19.9 (9.7–48.9)	12		0.081
	1998	9.8 (8.7–10.5)	6	a		12.6 (8.4–24.8)	13		
	2001	2.6 (1.2–6.2)	7	b		9.0 (5.6–10.6)	13		
	2002	3.6 (1.4–7.9)	6	b		6.8 (3.0–13.7)	13		
Copepods	1997				0.328	54.5 (33.1–68.5)	12		0.608
	1998	4.6 (2.9–5.2)	6			49.0 (37.5–58.7)	13		
	2001	6.2 (4.4–11.1)	7			60.1 (39.3–70.3)	13		
	2002	8.9 (6.0–16.9)	6			49.6 (38.1–56.5)	13		
Insect larvae	1998	96 (69–152)	3	a	0.006				
	2001	163 (74–178)	6	a					
	2002	511 (452–822)	6	b					
Molluscs	1998	58 (34–68)	3	a	0.023				
	2001	315 (126–585)	6	b					
	2002	641 (370–1267)	6	b					

Data for PAP are taken from Kasprzak *et al.* (2000); Hölker *et al.* (2002) and Haertel-Borer *et al.* (2005) (LIT: littoral zone; PEL: pelagic zone).

Where significant differences were found, pairwise comparisons were performed using the Nemenyi test (Ne). Significant differences between years are given by different lower case letters.

Table 2 Lake-wide total abundance (\pm SD) of roach, small perch and rudd derived from multiple mark-recapture experiments in Lake Großer Vätersee in the PAP (pikeperch absent period, spring 1998) and in the PPP (pikeperch present period, spring 2002)

Species	Period	Length (cm)	n	Abundance	t	P-value
Roach	PAP	7.0–15.9	19	42790 (\pm 1700)	9.76	0.001
Roach	PPP	6.0–15.9	13	25930 (\pm 7240)		
Perch	PAP	6.0–14.9	17	15650 (\pm 3960)	–4.39	0.001
Perch	PPP	6.0–14.9	16	21300 (\pm 3400)		
Rudd	PAP	7.5–12.5	15	2390 (\pm 720)	7.00	0.001
Rudd	PPP	6.0–13.0	7	410 (\pm 250)		

n, number of catch days.

Differences between PAP and PPP were analysed by Student's *t*-test. Data for PAP are taken from Haertel *et al.* (2002).

the littoral areas of the lake (H. Dörner, unpubl. data). Diel habitat use by rudd was not affected by the introduction of pikeperch (Fig. 2; Table 4). In both the PPP and the PAP, rudd were found exclusively in the littoral zone during the day, whereas they partly (10–30%) used the pelagic zone during the night.

Diet analysis of the predatory fish revealed that all three potential prey fish species within the size class 6–16 cm were taken (Fig. 3). The diet of pike consisted mainly of roach (mean: 13 440 year^{–1}) and small perch (8320 year^{–1}) during the PAP, but then decreased in

Table 1 Abundance (median plus inter-quartile range) of zooplankton (*Daphnia* sp., other cladocerans, copepods, nos. L^{–1}) and macrozoobenthos (insect larvae, molluscs, nos. m^{–2}) in Lake Großer Vätersee (May–October) in the PAP (1997/98) and the PPP (2001/02)

the PPP (1300 roach year^{–1} and 3900 small perch year^{–1}). The diet of large perch was dominated by roach (4160 year^{–1}) and small perch (3520 year^{–1}) during the PAP (Fig. 3). In contrast the contribution of roach decreased during the PPP (520 year^{–1}) and small perch dominated the diet (6200 year^{–1}). Pikeperch fed predominantly on small perch in the PPP (3810 year^{–1}; Fig. 3). The number of rudd consumed by pike increased from 410 year^{–1} in PAP to 1090 year^{–1} in the PPP. Whereas rudd were not found in the stomachs of large perch, 320 year^{–1} were consumed by pikeperch in the PPP.

Discussion

A major finding of our study is that different facultative planktivorous fish species responded differently to an overall change in predation risk in a whole lake. The behavioural response to pikeperch during the night ranged from a strong antipredator behaviour, reflected by reduced activity and habitat shifts towards the safer littoral zone (in roach) and reduced activity (in small perch), to a fixed behaviour with unchanged habitat use and activity (in rudd). Changes in resource density could also cause changes in behaviour (Reebs, 2002). In this study, however,

Table 3 Comparison of diel activity index A_i (multiplied by 1000) of roach, small perch and rudd (median plus interquartile range) in the PAP (pikeperch absent period, 1998) and the PPP (pikeperch present period, 2002) in Lake Großer Vätersee

Species	Time	PAP A_i	PPP A_i	Z	P-value
Roach	D	13.5 (8.1–57.8)	68.5 (7.4–91.6)	–1.086	0.318
	N	89.5 (79.4–141.1)	5.6 (0.9–12.0)	–3.130	0.001
Perch	D	260.7 (45.2–366.6)	133.9 (16.9–152.1)	–1.469	0.165
	N	11.5 (4.6–92.0)	0.0 (0.0–0.0)	–3.262	0.001
Rudd	D	0.0 (0.0–150.8)	211.8 (0.0–2529.4)	–1.795	0.097
	N	331.7 (15.1–688.4)	705.9 (117.6–1517.6)	–0.831	0.456

D, day; N, night; $n = 14$, Mann–Whitney U -test.

densities of the main food of planktivorous fish (zooplankton) declined in the littoral zones, and decreased marginally or tended to increase in the pelagic zone. Consequently, the pelagic zone rather than the littoral zone became more profitable in terms of zooplankton availability after the introduction of pikeperch. Thus, changes in resources did not underlie the observed behavioural changes following the introduction of pikeperch.

In roach, the stocking of pikeperch induced both reduced activity and a change in diel migration. The activity responses of roach to predators reported in the literature are equivocal. For example, daytime activity increased in response to large perch in wading pool experiments by Christensen & Persson (1993) whereas, in video-recorded laboratory trials, the swimming of roach declined in the presence of pike (Bean & Winfield, 1995). The predator-induced habitat shift from open water to safer habitats during the night in our field study agree with previous studies in the laboratory or field enclosures (Christensen & Persson, 1993; Bean & Winfield, 1995; Jacobsen & Perrow, 1998). In a further field study, Brabrand & Faafeng (1993) attributed a dramatic decline in the density of roach (>90%) in the pelagic zone, and an unchanged density in the littoral zone, after pikeperch introduction to a shift in diel habitat use and not to a loss of phenotypic plasticity (i.e. only non-migrating littoral roach survived in the system). Our whole-lake experiment is, however, the first which clearly validates a habitat shift induced in roach by pikeperch under natural conditions.

In small perch, there was a predator-mediated response in one of the two measured traits: activity. A predator-mediated decrease in activity has been documented previously in laboratory trials and field enclosure experiments (Christensen & Persson, 1993; Bean & Winfield, 1995; Jacobsen & Berg, 1998). Here, we found similar responses in a whole-lake experiment. Therefore, small perch can apparently demon-

strate adaptive responses to a single additional predator, even in a complex natural setting with other pre-existing predators. Further, this response seems to persist over the long (seasonal) time scales which are important to abundance and dynamics. The primary use of littoral habitat by small perch in the presence of predators is consistent with previous research (Christensen & Persson, 1993; Jacobsen & Perrow, 1998; Okun & Mehner, 2005).

In contrast to roach and small perch, rudd did not respond to the changed predatory environment, corresponding to previous research. In a field enclosure experiment, for example, rudd did not change habitat use to the presence of pikeperch and pike if artificial vegetation was available (Greenberg, Pazkowski & Tonn, 1995). In laboratory trials, rudd also maintained their activity in both open and structured environments in the presence of pike (Bean & Winfield, 1995). Since there are no field studies reporting a preference of the pelagic zone by rudd they do not appear to show a behavioural response to predation risk. This is discussed further below.

In contrast to the drastic behavioural response of prey during the night, when only one predator (pikeperch) was strongly active, activity and habitat use by all three planktivorous fish remained almost unchanged during the day throughout the study. This may be explained by the different effect of two predators hunting concurrently during the day in the PAP and three predators in the PPP compared with the effect of a single predator alone. While large perch and pikeperch foraged mainly in the pelagic zone, pike were restricted to the littoral zone. Based on experimental findings with single predators, both small perch and roach should move into or stay close to vegetation in the presence of large perch, but should use the open water in the presence of pike (Christensen & Persson, 1993; Eklöv & VanKooten, 2001). However, a multiple predator situation, as in Lake Großer Vätersee, can lead to higher or lower

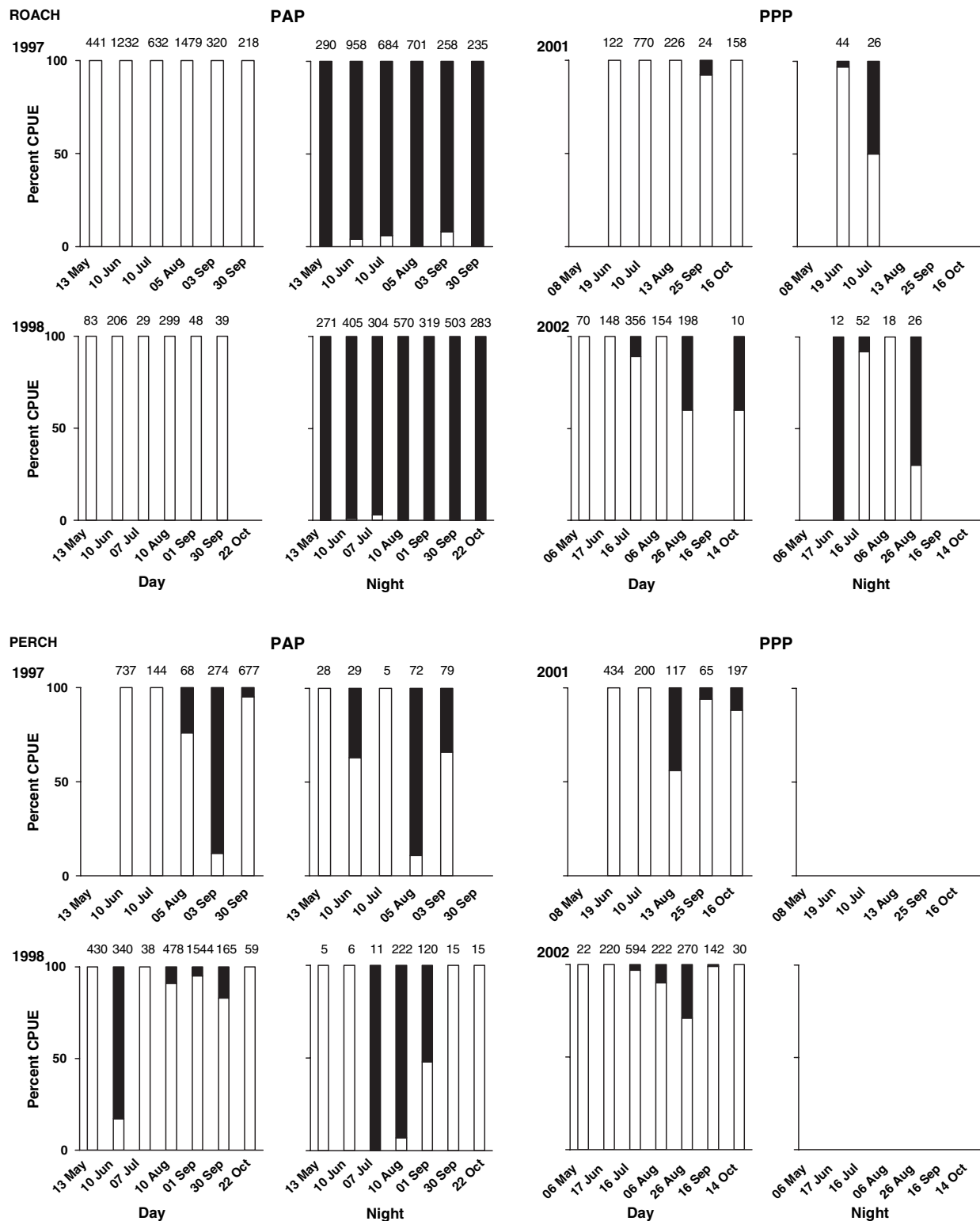


Fig. 1 Diel habitat use expressed as the percentage of the total (day and night) catch of roach and small perch taken in two habitats in Lake Großer Vätersee, in the PAP (pikeperch absent period, 1997/98) and in the PPP (pikeperch present period, 2001/02). Data for roach in the PAP are taken from Haertel *et al.* (2002). White columns: littoral zone; black columns: pelagic zone. Numbers on top of columns: sample sizes [catch per unit effort (CPUE)].

Table 4 Comparison of diel habitat use of roach, small perch, and rudd (median plus interquartile range) based on percentages of total catch in the PAP (pikeperch absent period, 1997/98) and the PPP (pikeperch present period, 2001/02) in Lake Großer Vätersee

Species	Period	Time	% CPUE LIT	n	Z	P-value
Roach	PAP	D	100 (100–100)	12		
	PPP	D	100 (89–100)	11	–2.236	0.151
	PAP	N	0 (0–4)	13		
	PPP	N	71 (23–98)	6	–2.782	0.007
Perch	PAP	D	95 (78–100)	12		
	PPP	D	99 (89–100)	13	–0.569	0.611
	PAP	N	83 (20–100)	12		
	PPP	N	–	0		–
Rudd	PAP	D	100 (100–100)	6		
	PPP	D	100 (94–100)	5	–1.095	0.662
	PAP	N	90 (60–95)	12		
	PPP	N	69 (42–96)	11	–0.432	0.695

D, day; N, night; CPUE, catch per unit effort; LIT, littoral zone; Mann–Whitney *U*-test, cf. Figs 1 & 2).

predation than predicted by a simple addition of individual predator effects. In a littoral enclosure experiment with pike and large perch, Eklöv & VanKooten (2001) found an antipredator behaviour

of roach that actually made them more susceptible to pike predation alone. In their experiment, roach were repeatedly chased into the refuge (from perch) where pike were located. Relyea (2003) observed that tadpoles in a multiple predator environment developed phenotypes that were similar to those induced by the more dangerous predator alone. He suggested that the prey perceive the risk of combined predators as being similar to the risk of the most dangerous predator in the pair, and not as a summed or averaged predation risk. Similarly, roach and small perch in Lake Großer Vätersee might perceive the risk from the more active, and thus probably more detectable, large perch and pikeperch as greater than that imposed by the less active pike. As a sit and wait predator, pike might produce less visual and chemical cues. The observed diurnal littoral habitat use by both roach and small perch in this complex predator situation would then be consistent with a response to the predator imposing the highest perceived risk.

Our study provides an example of a relationship between fitness benefits (reduced mortality) and the magnitude of behavioural responses to predation risk.

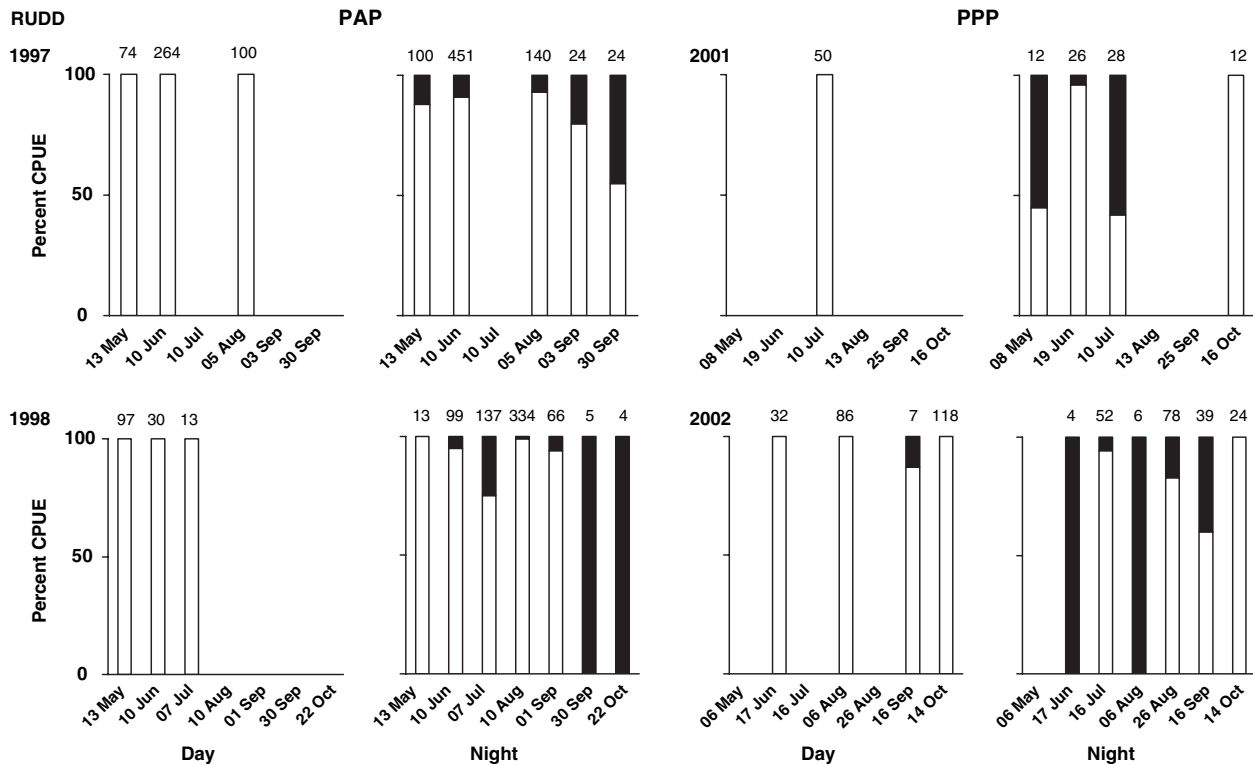


Fig. 2 Diel habitat use expressed as the percentage of the total (day and night) catch of rudd taken in two habitats in Lake Großer Vätersee, in the PAP (pikeperch absent period, 1997/98) and in the PPP (pikeperch present period, 2001/02). White columns: littoral zone; black columns: pelagic zone. Numbers on top of columns: sample sizes [catch per unit effort (CPUE)].

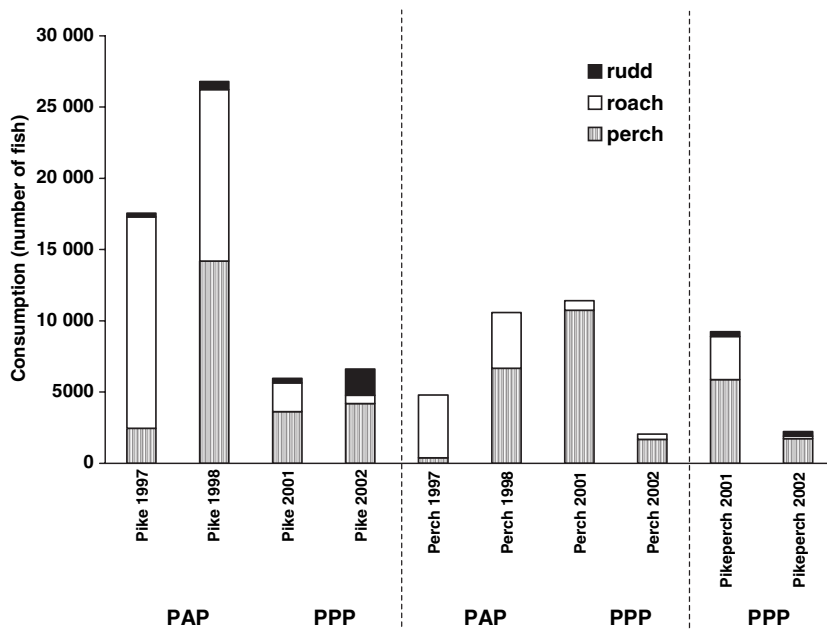


Fig. 3 Consumption of three planktivorous fish by predators in Lake Großer Vätersee in the PAP (pikeperch absent period, 1997/98) and in the PPP (pikeperch present period, 2001/02). Note: only the prey size class 6–16 cm is considered.

With decreasing strength of antipredator responses, the predator-mediated density changes ranged from an increase or a slight decrease in small perch and roach, to a drastic fall of more than 80% in the rudd population. Many prey organisms respond to predators by adopting behaviour that decreases encounter rate with predators. In general, a direct relationship between fitness and the magnitude of prey responses could be expected (Lima, 1998). For example, in a multi-species comparison using tadpoles, Relyea (2001) detected a correlation between behavioural modifications and mortality but not between plastic morphological traits and mortality. On the other hand, Wohlfahrt *et al.* (2006) found that fitness and the magnitude of behavioural response were not correlated in five different larval odonates when subjected to risk from fish predation. They argue that the consequence for fitness of anti-predator responses depend more on the particular predator-prey pair rather than the magnitude of the behavioural response. Only a few laboratory experiments, and to our knowledge no field studies with multiple prey and predator species, have been designed to investigate the relationship between fitness and the magnitude of prey responses. It should be mentioned, however, that in our study the growth of underyearling fish was sufficient to 'grow into' the study size range 6–16 cm. Thus, recruitment may have contributed to the observed changes in population abundance of roach

and perch: nevertheless, the lack of a strong negative effect on fitness on these species is clear. Further, recruitment cannot explain the decrease in rudd.

The apparent inability of rudd to respond to increased predation risk, and the severe reduction in its abundance, suggests a maladaptive inflexibility in this species. Most research on plasticity focuses on putatively adaptive responses to environmental challenges (Miner *et al.*, 2005). However, it is equally important to investigate the ecological consequences of an inability to respond, which is likely to be common (Langerhans & DeWitt, 2002). This is especially true for maladaptive behaviour that might amplify the effects of environmental change through negative effects on individuals (Miner *et al.*, 2005). The apparent inability of rudd to respond to the enhanced risk could result from three mechanisms: (i) phylogenetic inertia; (ii) naïvity to introduced predators or (iii) behavioural syndromes (Sih *et al.*, 2000; Caudill & Peckarsky, 2003; Sih *et al.*, 2004).

Fixed behaviour caused by phylogenetic inertia (mechanism 1) means that traits which are adaptive in one habitat can become deleterious in another. For example, the ineffective antipredator behaviour of a salamander that coexists with a fish could partly be explained by its recent divergence from a sister species that did not coexist with that predator (Sih *et al.*, 2000). However, the radiation within the Leuciscinae leading to the genus *Scardinius* is very old (mid-Miocene;

Zardoya & Doadrio, 1999). Thus, rudd did not diverge recently from a sister species naïve to pikeperch, so that the phylogenetic inertia hypothesis is unlikely to explain the maladaptive behaviour of rudd.

Prey naïve to predators (mechanism 2) often show ineffective antipredator behaviours relative to similar prey exposed to predators (Riechert, 1993; McPeck, Schrot & Brown, 1996). Accordingly, introduced predators often have major impacts on naïve prey (Clavero & García-Berthou, 2005). The rudd population of Großer Vätersee was naïve to the experimental introduction of pikeperch, which could be responsible for its obviously maladaptive behaviour. However, rudd did not respond to the increased predation rate in 2002 by pike, to which it was not naïve. Accordingly, it is doubtful that the lack of response in rudd to pikeperch results from its naïvety to the non-native predator.

We believe that the most likely explanation of the ineffective antipredator behaviour of rudd is based on a 'behavioural syndrome' (mechanism 3). A behavioural syndrome refers to correlations between behaviours expressed in different contexts (e.g. feeding activity, predator avoidance) across different situations (different densities of predators), which could appear non-adaptive in any particular context (e.g. predator avoidance; Sih *et al.*, 2004). Many studies have shown that increased refuge use or reduced activity conflict with feeding efficiency (Sih, 1987; Lima & Dill, 1990; Lima, 1998). In the theoretical case of unlimited plasticity in activity and refuge use, a species should be able both to reduce activity when exposed to predation risk and to increase feeding activity in competitive or ephemeral habitats. However, the limited plasticity associated with a behavioural syndrome appears to limit species to particular habitats (Sih *et al.*, 2004). Thus, selection favouring high feeding success in a particular habitat could explain a lack of antipredator behaviour. Among the fish species in European waters, rudd is the only specialist herbivore (Lammens & Hoogenboezem, 1991), making it competitively superior in habitats with a high availability of plant material. Rudd may have to increase their feeding, however, to compensate for a low quality diet (*cf.* Hölker *et al.*, 2002). This, in turn, may force them to spend more time feeding, thus diminishing vigilance. Accordingly, a fixed association with vegetation may enable rudd to maximize food uptake and to enhance its

competitiveness. This advantage may come at the cost of high predation risk and an inability to respond to predation risk. In European lakes, piscivorous fish may control planktivorous fish stocks and their annual production at ratios of about 25% biomass piscivorous fish to 75% biomass planktivorous fish (Mehner *et al.*, 2004). In Lake Großer Vätersee, the piscivorous fish biomass accounted for as much as 30% of total fish biomass in the PAP, and was increased to between 42% and 64% after the introduction of pikeperch. Hence, the fixed behaviour of rudd may have become maladaptive under the high predation pressure imposed in the lake.

In conclusion, our whole lake study provided empirical evidence that antipredator capacities can play an important role in accounting for the variation among planktivorous fish in responding to predation risk. In our study, these differences between the prey species were associated with numerical changes in the population, in that the species that did not respond to increased risk suffered the greatest population decline. Behavioural syndromes might explain behaviours that appear strikingly non-adaptive in an isolated context (Sih *et al.*, 2004), such as the lack of response by rudd to increased predation risk. Previous studies on behavioural syndromes have focused on a few species, primarily in laboratory conditions (Sih *et al.*, 2004). Further work, particularly in the field, is needed to identify which behaviours are correlated under which conditions, and should ask how stable are behavioural syndromes from an evolutionary point of view.

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